Final Report – Western National Parks Association
Effects of small mammals on post-fire vegetation recovery in the Mojave Desert

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Background

Although arid and semiarid ecosystems are usually considered too unproductive to support high fuel loads, episodic wildfires can still have catastrophic effects (Westerling et al. 2003, Brooks et al. 2004, Letnic et al. 2005). In the Mojave Desert, large amounts of rainfall in the winter of 2004-05 resulted in unusually high plant growth, especially at higher elevations. On 22 June 2005, dry lightening strikes ignited a series of large fires in the central Mojave National Preserve (MNP). When these fires, collectively known as the Hackberry Complex Fire (HCF), were finally contained on 27 June, some 31,580 ha had burned, mostly in mixed sagebrush (*Artemesia*)-juniper (*Juniperus*) and other woodland and scrub plant communities.

The HCF was the largest recorded for the eastern Mojave, and is expected to have long-lasting effects on the character, management and ecology of this portion of the MNP. In particular, there are concerns that fire will facilitate continued invasion by exotic plants (Lovich and Bainbridge 1999). Herbivory by native ungulates and rabbits and granivory by nocturnal rodents may also significantly influence the re-growth of vegetation and, potentially, the spread of exotic annual grasses such as *Bromus rubens* and *Schismus* spp., which out-compete native plants and are the most important sources of fuels (Brooks 2002). Compared to other arid and semiarid systems (e.g., Schwilk and Keeley 1998, Olson et al. 2003, Letnic et al. 2005), however, the effects of fire on small mammal communities and the role of small mammals in post-fire vegetation recovery in the Mojave Desert are poorly understood. For example, selective granivory can alter local plant communities and the trajectory of desert ecosystems (Brown and Heske 1990). Although rodent species are differentially affected by fire (McGee 1982, Schwilk and Keeley 1998, Esque et al. 2003), individuals that survive the immediate effects of fire may accumulate in remnant unburned patches, resulting in high population densities and a greater impact on local plants and seed resources. In theory, the high densities of rodents may also impose high foraging pressure on plants and seeds in the adjacent burned areas, which, depending on the source of new seeds and the relative preference of rodents for exotic vs. native species, may result in very different plant communities near the edge than farther into the burn. Understanding the effects of fire on species composition and relative abundance of small mammals, and the spatial pattern of foraging behavior and seed removal, may have important implications for the use of fire as a tool to control exotic plant invasions and for the re-establishment of native desert plant communities following catastrophic fire.

I studied the effects of fire-mediated changes in habitat and resources on the abundance and foraging activity of small mammals, and on their possible effects on post-fire vegetation recovery of vegetation in sagebrush-juniper vegetation in the MNP. The specific objectives of the project were to determine:

- relative abundance and community attributes of small mammals in burned and unburned areas of sagebrush-juniper vegetation, and examine how these change across the transition (edge) between burned and unburned vegetation;

- the pattern of seed removal by small mammals across the burn edge to estimate potential impact of granivores on the seed bank;

- the effects of small and large herbivores and granivores on vegetation recovery in burned areas compared to the burn edge.

Field work on the project began in May 2006, 11 months after the HCF, and, except for the ongoing experimental studies of vegetation recovery, was completed by August 2007. Most of the field work was conducted by a former CSUF Master's student (C. Moore).

Methods

The research site was in the Mid Hills region of the Mojave National Preserve (MNP), California (35º9' N, 115º23' W), at elevations between 1500-1600 m. Mean annual precipitation at the nearby Mid Hills Campground is 264 mm, with a mean winter daily minimum and summer daily maximum of 3.2°C and 34.3°C, respectively. Most precipitation falls during the winter months (November–March), although there are often summer thunderstorms as well. The dominant vegetation is big sagebrush (*Artemisia tridentata*) and Utah juniper (*Juniperus osteosperma*). Other abundant perennials include desert bitterbrush (*Purshia tridentata*), Nevada ephedra (*Ephedra nevadensis*), banana yucca (*Yucca baccata*), turpentinebroom (*Thamnosma montana*), as well as a number of forbs and grasses. Abundant annuals include western tansymustard (*Descuraina pinnata*), birdnest buckwheat (*Eriogonum nidularium*), storksbill (*Erodium cicutarium*), and Fremont's phacelia (*Phacelia fremontii*).

In May 2006, four study plots were established at edge of the HCF. Plots were 1.60 ha (80 x 200 m), with the long axis perpendicular to and centered on the edge of the burn. Plots were at least 100 m away from each other and roads. Trapping grids (5 x 11; 66 stations) were established on each plot to estimate relative abundance and diversity of nocturnal rodents. One extra-long Sherman live-trap was placed at each station, which were 20 m apart (Fig. 1). Traps were baited with irradiated birdseed at dusk and checked at dawn. Trapping sessions were 4 consecutive nights. Each individual captured was marked with a uniquely numbered aluminum ear tag and released. All animal handling procedures were approved by the Institutional Animal Care and Use Committee at CSUF.

Two trapping sessions were conducted on each plot from June–August 2006 and May–August 2007, for a total of 3,520 trap-nights. On each plot, trapping sessions were conducted during full and new moon periods to account for differences in rodent activity associated with moonlight. I used the number of unique individuals captured in each location (burned, 40-100 m, trap rows 1-4; edge, 0, $\pm$20 m, traps 5-7; burned, 40-100 m, traps 8-11) and plot during each trapping session, based on their location of first capture, as an estimate of relative abundance. In addition, four smaller grids (5 x 4 stations at 20-m intervals) were established in an area of Joshua tree woodland that also burned during the HCF. Two plots were in burned vegetation and two were in unburned vegetation, with plots approximately 100 m apart. These grids were trapped twice between June and August 2006, with the goal of comparing rodent communities in burned and unburned areas of Joshua tree woodlands to that in sagebrush vegetation.

To determine spatial patterns of seed removal across the sagebrush burn transition, foraging activity was measured in artificial seed trays placed in three parallel transects, 20 m apart and perpendicular to the burn edge, on each of the 4 large study plots. Trays were placed at 80, 40, 20 and 10 m into the burn, at the edge of the burn (0 m), and at 20 and 80 m into unburned sagebrush vegetation (Fig. 1), for a total of 21 trays per plot. Seed trays were plastic plant saucers (36 cm diameter, 4 cm deep) filled with 2 L of pre-sifted sand. Trays were set at dusk by mixing 4.00 g of irradiated millet into the sand, and smoothing the surface so that foraging activity could be detected. Trays were collected at dawn and the sand was sieved to collect the remaining seed, which was weighed to estimate the amount of seed removed. On each plot, trays were set for 2 consecutive nights during full and new moon periods in June and July 2006. The difference between the first and second night reflect the time needed for rodents to discover seed trays, which would be expected to be longer on Night 1, i.e. fewer trays would be discovered, especially if moonlight reduced aboveground foraging activity.

To determine the effects of herbivores and granivores on vegetation recovery, in March 2007 exclosures were established on 2 of the sagebrush study plots, as well as one new plot that crossed the boundary of the Wildhorse Fire (WHF), which burned sagebrush-juniper vegetation in July 2002 in the same area. Exclosures were constructed of 1.3-cm mesh hardware cloth and were 60 x 60 cm (0.36 m^2) and 30 cm high. The exclosure walls were buried 10 cm into the ground. Three different types of exclosures were used. One (N) had solid walls and a roof to exclude all herbivores, including rodents, rabbits, deer and cattle. Another (R) was similar to N but had two 8 x 8 cm holes on each wall, which excluded larger herbivores but allowed access to large rodents (*Dipodomys panamintinus*, *Neotoma lepida*). The third type (C) was a control that was similar to R but without a roof, to permit access to all herbivores while mimicking any effects of the exclosure walls.

Exclosures were placed at the burn edge and 100 m into the burn on each plot. Five stations, each 20 m apart, were established at each location. Each station had one of each type of exclosure, set at random locations approximately 2 m apart. Therefore, there were a total of 10 exclosures of each type at edge and burn locations of the HCF plots, and 5 exclosures of each type at edge and burned locations on the WHF plot.

Vegetation in exclosures was measured beginning in May 2007 and has continued intermittently since. Percent canopy cover, number of individual plants and species richness was measured in a 40 x 40 m (0.16 m^2) quadrat in the center of each exclosure. The effects of small and large herbivores was estimated by comparing plant percent cover, plant density and species richness between exclosures and controls that were accessible to all herbivores. The difference between N and C exclosures reflected the effects of all herbivores on vegetation; the difference between R and C exclosures was used to estimate the effects of large herbivores only; and the difference between N and R exclosures estimated the effects of rodents. To account for local effects, differences were calculated for each set of exclosures (station) during each sampling period; statistical analyses were conducted on mean differences. Data from May 2007, only ~1 month after exclosures were in place, were excluded from statistical analyses. Because sample size (n=5 per type) and therefore, power, was low for WHF plots, I used $\alpha = 0.10$ to evaluate whether results were statistically significant. Here, I focus on percent cover and species richness as response variables.

Results

Heteromyid rodents were the most abundant species captured in sagebrush areas, with *D. panamintinus* (DIPA) and *D. merriami* (DIME) representing 65% and 12% of the 428 individuals captured. Three species of *Peromyscus* (*maniculatus*, *crinitus*, *truei*), here considered collectively (PESP), were the most abundant cricetids (14% of individuals), followed by *N. lepida* (6%). *Perognathus longimembris* (PELO) and *Onychomys torridus* (ONTO) made up the remaining 3% of individuals. The rodent community in Joshua tree woodlands was similar, except that *D. merriami* was more abundant than *D. panamintinus*, and that *Chaetodipus penicillatus* was also captured.

By all three community metrics examined (N0, N1, N2), rodent diversity was highest in unburned vegetation, intermediate at the edge, and lowest in the burn (Table 1). For all three indices, diversity was significantly higher in unburned vegetation than at the edge and burned areas (ANOVA, $P<0.003$), which were not significantly different from each other. Rodent diversity was significantly higher in 2006 than 2007 for all three vegetation types ($P<0.020$). Graphically, a non-metric multidimensional scaling (MDS) plot, followed by an analysis-of-similarity (ANOSIM) in PRIMER (Clarke and Gorley 2006), indicated significant clustering of rodent communities both by year ($P=0.011$) and vegetation type ($P=0.001$; Fig. 2), revealing that community structure differed among vegetation types. Rodent diversity in unburned sagebrush was similar to that in unburned Joshua tree woodland (Table 1), but burned areas of Joshua tree woodlands retained higher rodent diversity than in burned sagebrush.

In both years, DIPA was the only species captured in high numbers in burned sagebrush areas (Fig. 3), and their abundance generally declined toward the edge of the burn and in unburned vegetation, especially in 2007. DIME was most abundant at the edge and in unburned vegetation (Fig. 3). Cricetids were more abundant and widespread in 2006 than in 2007, and tended to be restricted to unburned areas.

Rates of seed removal were usually highest on dark, new-moon nights than on full-moon nights, a pattern that was particularly evident in the more open, burned vegetation (Fig. 4). On full-moon nights, the amount of seed removed was lowest in the burn, and increased toward the burn edge. In contrast, on new-moon nights, rodents, presumably DIPA, consumed large amounts of seed in the burn (Fig. 4). On the first night of trials, significantly more seed was consumed on new- than full-moon nights (ANOVA, $P = 0.021$), but there was no significant difference between distance categories ($P = 0.145$). On the second night, when most trays would have been discovered by rodents, more seeds were eaten on new moon nights ($P<0.001$) and at the burn edge ($P=0.002$). On Night 2, a significant interaction between moonlight and distance ($P<0.001$) also indicated significant differences between distances on full-moon nights (Fig. 4), but no distance effects on new moon nights ($P>0.05$).

At the HCF burn sites, the consistently positive differences between plant cover in N and C exclosures (Fig. 5, top) indicated that herbivores collectively significantly reduced plant cover by approximately 7% during the study period (paired t-tests, N-C; $P<0.05$). The effects were similar in the burn and at the edge ($P=0.947$; Fig. 5). In contrast, excluding large herbivores only (R-C) significantly increased plant cover in the burn ($P=0.035$), but not at the edge ($P=0.151$; Fig. 5, bottom), and the difference in plant cover between R and C exclosures was consistently higher in the burn ($P=0.030$). This could have resulted from higher foraging activity of large herbivores in the burn; however, the effect of rodents (N-R) was also significantly higher at the edge than in the burn ($P<0.001$; Fig. 6, top left), which likely contributed to lower cover in both R and C exclosures. Excluding both large and all herbivores combined reduced species richness in the burn relative to the edge ($P<0.034$), suggesting that herbivores may mediate competition between plants. In contrast, rodents had little effect on plant species richness in either the burn or at the HCF edge (N-R, $P=0.450$; Fig. 6, top right).

Herbivores, and especially rodents, had markedly different effects at the older, WHF burn site. Excluding all herbivores significantly increased plant cover and species richness vs. controls in the burn ($P<0.076$), but not at the edge ($P>0.209$). Excluding only large herbivores had no significant effect on plant cover or species richness, either in the burn or at the edge ($P>0.10$). Whereas the effect of rodents on plant cover was greater at the edge than in the burn at the HCF (Fig. 6, top left), at the WHF site this pattern was reversed, with the exclusion of rodents resulting in an increase in cover in the burn, but decreased cover at the edge ($P=0.009$; Fig. 6, bottom left). Similarly, excluding rodents increased plant species richness in the burn, but decreased it at the edge ($P=0.012$; Fig. 6, bottom right).

Discussion

Because field work on this project began in May 2006, some 11 months after the HCF, it is not possible to know how much mortality of small mammals was caused directly by the fire. Nonetheless, despite the near absence of perennial vegetation, rodents inhabited the burned sagebrush areas in relatively high numbers. *Dipodomys panamintinus* was the only species captured consistently far into the burn, although it was also present in lower numbers at the edge and in unburned areas. Assuming that, prior to the fire, rodent communities in the burn were similar to those in the unburned vegetation, cricetids and notably, *N. lepida*, likely suffered most from the fire. This was particularly true in 2007, when populations of most species and rodent diversity were much lower than in 2006. The difference between years may be due to worsening resource conditions during the 2 years after the fire, or may simply reflect inter-annual variation in resource availability and therefore rodent productivity.

By all community indices examined, the HCF significantly reduced rodent diversity compared to the unburned sagebrush. Diversity was somewhat higher at the edge than 100 m into the burn, but the edge community more closely resembled that in the burn than in the unburned vegetation, where cricetids were dominant and diversity was consistently highest.

Dipodomys merriami, a smaller kangaroo rat that would be expected to be competitively subordinate to *D. panamintinus*, tended to be most abundant at the edge, possibly responding to the decline in abundance of its larger congener near the edge, especially in 2007.

Although species composition clearly differed between the edge and burned and unburned areas, combining all species, total rodent abundance varied little across the study plots. Presumably as a result of the high numbers of *D. panamintinus* in the burn, there was surprisingly little variation in seed removal on dark, new-moon nights between burned, edge and unburned vegetation. Even seeds 80 m from the unburned refugia were discovered and consumed on dark nights. However, indirect effects on the HCF on rodent foraging activity were apparent on full-moon nights, when significantly fewer seeds were removed in the burn. This difference can probably be attributed to the loss of protective overhead cover as a result of the fire, which could make rodents more sensitive to predation risk on brightly lit nights (e.g. Price et al. 1984, Longland et al. 1991). Because potential granivores were abundant at all distances from the burn edge, it seems likely that the increasing seed removal rates with decreasing distance into the burn reflects the tendency of rodents living at the edge or in unburned vegetation to not wander far from the safety of the edge on full-moon nights.

The extent and mechanisms by which small mammals influence vegetation recovery following fires in high-elevation sagebrush habitats are not yet clear, and this aspect of the project is ongoing. However, results thus far from my exclosure experiments suggest that large herbivores and granivores influence both plant cover and species richness. Excluding herbivores consistently led to increases in plant cover in both the burn and at the edge. The high rates of seed removal observed at the edge during seed tray trials may be translated into larger effects of rodent exclusion on plant cover near the HCF edge than in the burn itself, though plant species richness was not different. In addition, the effects of rodents were more pronounced on the 2002 WHF, suggesting that, given the low productivity of the Mojave Desert, it may take several years to observe significant changes in plant responses to herbivores and granivores. In particular, the relative decrease in cover and plant species richness in rodent exclosures at the edge suggests some positive effects of rodents that are only manifest over longer periods.

In conclusion, I found that granivorous rodents continued to live in high numbers in the burned areas of the HCF and that, at least on dark nights, rates of seed removal were comparable to those near the edge of the unburned vegetation. This suggests that, for restoration efforts, planting seeds far into a burn does not necessarily make them safer from granivores. Combining across nights, however, the higher rates of seed removal at the edge, combined with the diversity of small mammals in remnant unburned patches, implies that seeds and seedlings planted near the edge of a fire may be at greater risk of consumption or caching. Ultimately, rodents may have a facilitative effect on plant recovery, as suggested by results from the WHF exclosure experiments, though it is not known if these effects benefit native or exotic plant species more. Unfortunately, data on the plant percent cover and density were not collected separately for each species, information that is critical to determine if there are differences in species composition, and especially in the abundance of exotic species, between exclosures. Future sampling of plant responses in exclosures will examine possible differences in plant species composition between exclosures, as well as between the burn and edge.

References

Brown and Heske 1990. Science 250:1705; Brooks 2002. Ecol. Appl. 12:1088; Brooks et al. 2004. Bioscience 54:677; Esque et al. 2003. SW Nat. 48:103; Clarke and Gorley 2006. PRIMER-E, v. 6.1.5; Letnic et al. 2005. J. Mammal. 86:689; Longland et al. 1991. Ecology 72:2261; Lovich and Bainbridge. 1999. Environ. Manage. 24:309; McGee. 1982. J. Range Manage 35:177; Olson et al. 2003. West. NA Nat. 63:50; Price et al. 1984. J. Mammal. 65:353; Schwilk and Keeley. 1998. SW Nat. 43:480; Westerling et al. 2003. BAMS May:595.

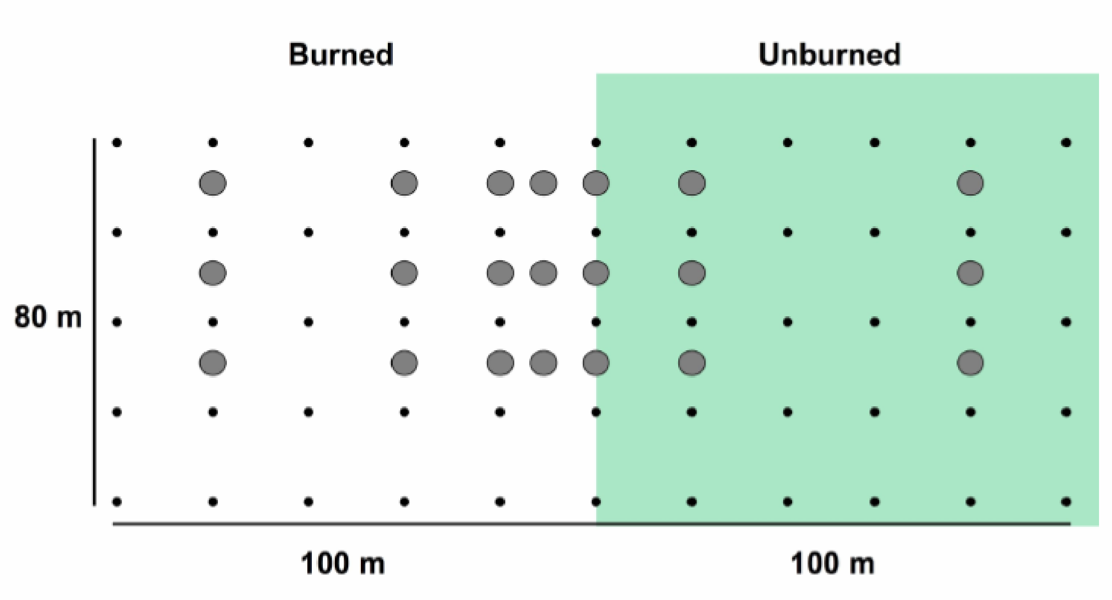


Fig. 1. Layout of 1.60-ha plots in sagebrush-juniper vegetation in high-elevation Mojave Desert. The small black circles represent trap stations spaced 20 m apart (80 x 200 m grid), for a total of 55 Sherman live traps per plot. The larger gray circles indicate locations of seed trays placed 80, 40, 20, and 10 m into the burn, at the burn-unburned edge, and 20 and 80 m into the unburned vegetation.

Table 1. Mean abundance (N) and community diversity indices (species richness N0; Hill's N1; Hill's N2) on 4 1.60–ha study plots that spanned the transition from burned to unburned sagebrush in 2006 and 2007. For comparison, results from trapping in burned and unburned Joshua tree woodlands in 2006 are also included.

Vegetation/ year/variable	Burn (40-100 m)	Edge ($\pm$20 m)	Unburned (40-100 m)
Sagebrush (n=4 plots)			
2006			
N	10.25 (1.80)	7.75 (0.48)	10.75 (1.80)
N0	3.00 (0.41)	3.00 (0.00)	4.25 (0.48)
N1	1.91 (0.35)	2.63 (0.15)	3.49 (0.37)
N2	1.60 (0.25)	2.47 (0.19)	3.12 (0.31)
2007			
N	12.25 (0.48)	6.25 (0.75)	8.00 (0.82)
N0	2.00 (0.71)	2.25 (0.25)	3.75 (0.25)
N1	1.38 (0.22)	1.65 (0.19)	3.31 (0.28)
N2	1.23 (0.13)	1.45 (0.16)	3.06 (0.29)
Joshua tree (n=2 plots)			
2006			
N	25.50 (1.50)	-	13.50 (0.50)
N0	4.50 (0.50)	-	4.00 (0.00)
N1	2.38 (0.47)	-	3.23 (0.15)
N2	1.90 (0.38)	-	2.89 (0.11)

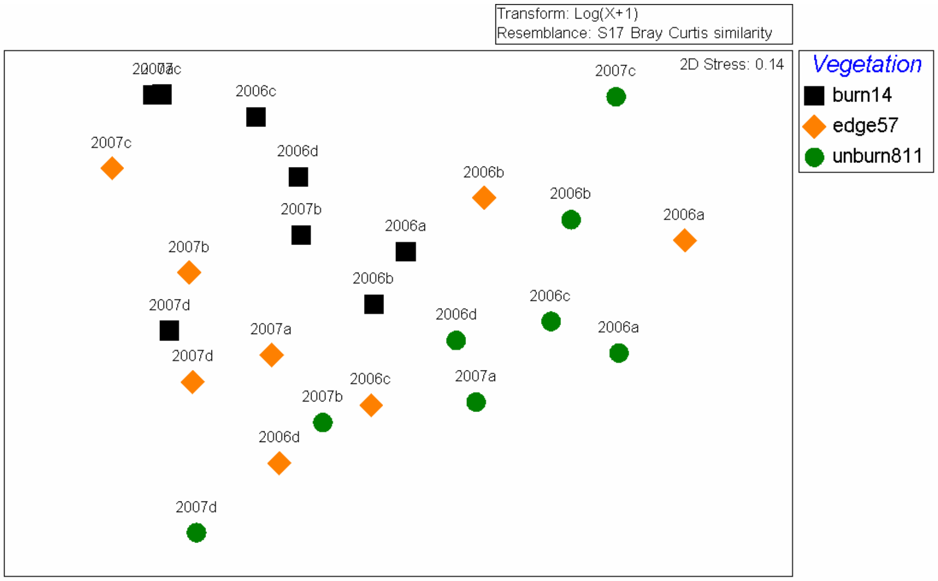


Fig. 2. MDS plot showing the relationships between rodent communities in burned, edge and unburned sagebrush in 2006 and 2007. Each point represents a different plot (a-d), taking the mean of numbers of individuals caught during trapping sessions within a year.

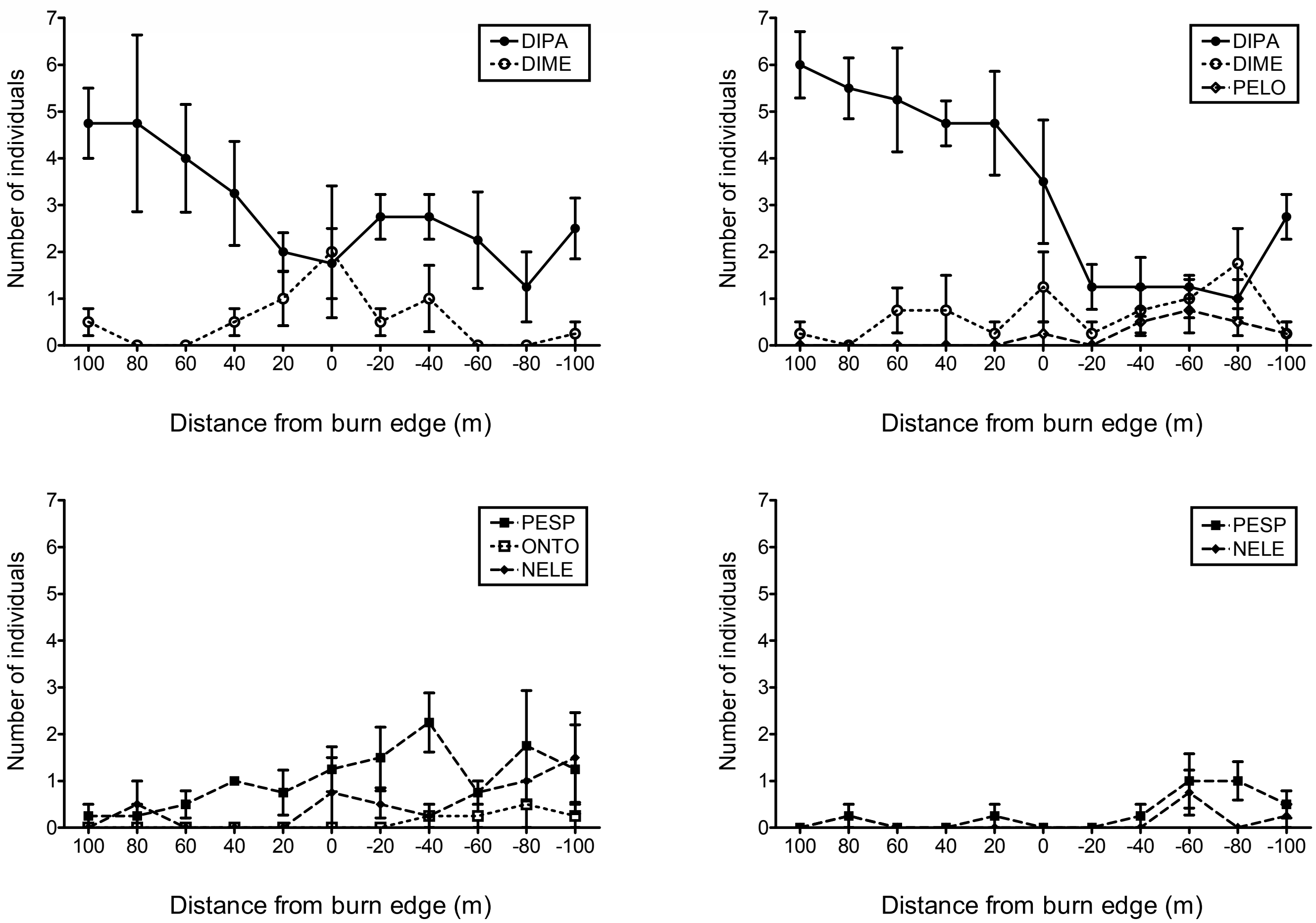


Fig. 3. Relative abundance (mean + 1 SE) of rodents with distance along a transition from burned (positive values) to unburned vegetation (negative values) sagebrush vegetation in 2006 (left panels) and 2007 (right panels).

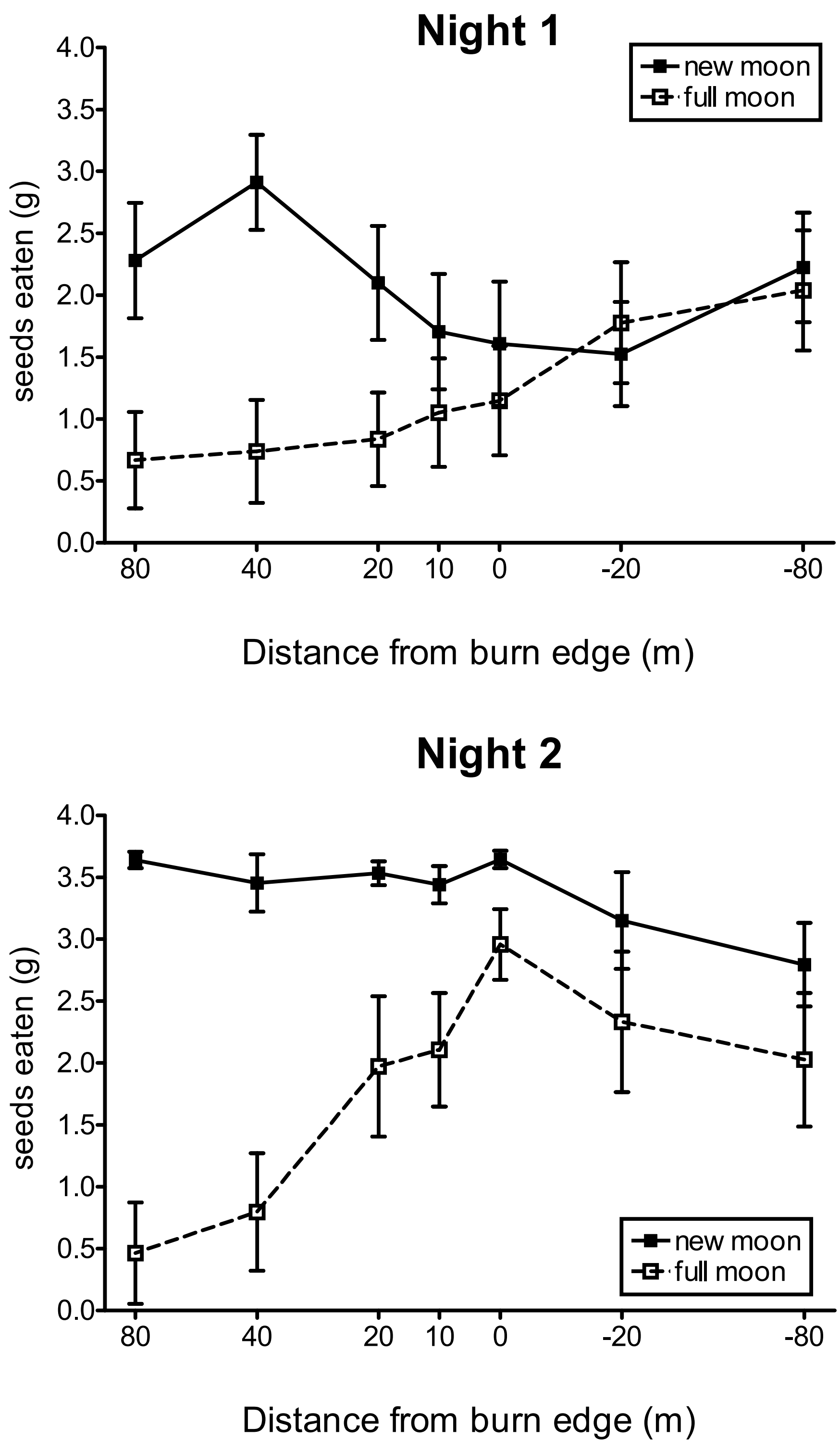
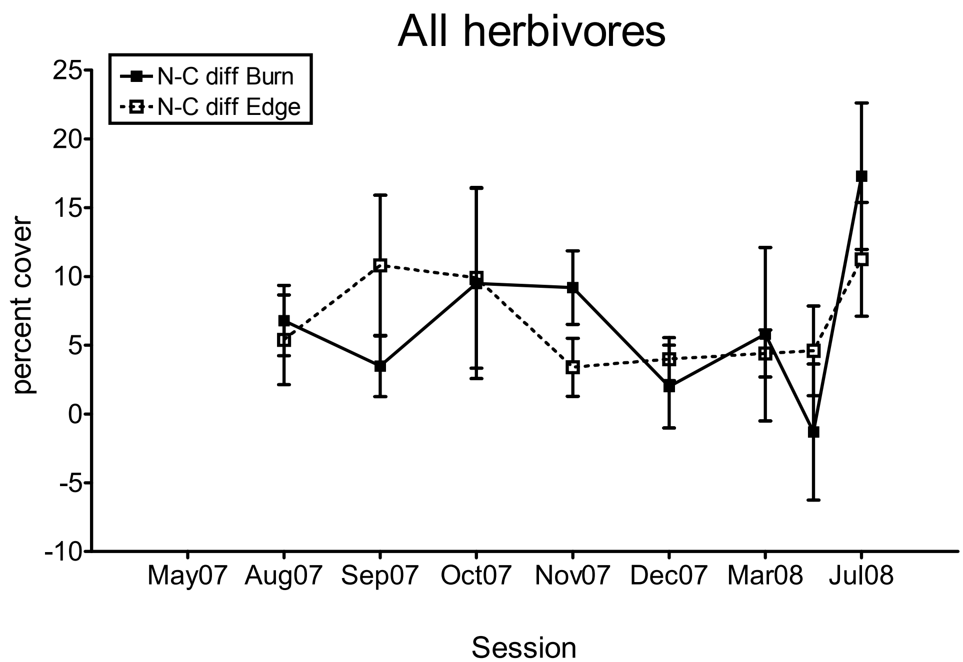


Fig. 4. Amounts of seed removed (mean $\pm$ 1 SE) in 2006 from artificial seed trays with distance from the edge of the HCF burn in sagebrush vegetation. Trials were run for 2 consecutive nights in each season on 4 study plots, with a total of n=9-12 trays per distance class for each moon phase.



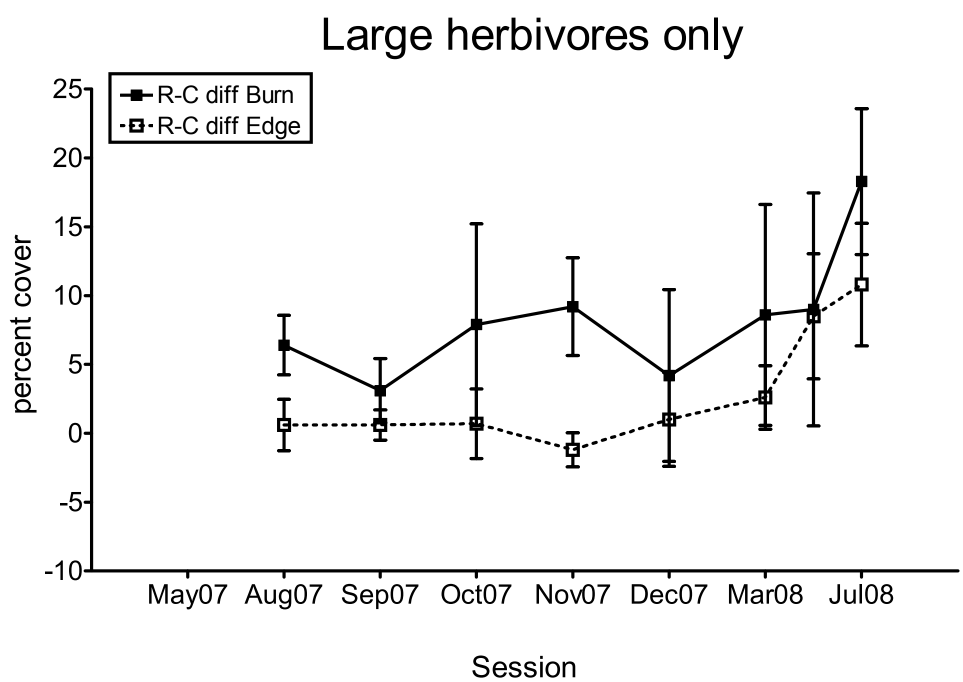


Fig. 5. Effects of excluding all herbivores (top) and large herbivores only (bottom) on percent cover of plants 100 m into the 2005 HCF and at the fire's edge. Effects were calculated as the difference between N and C exclosures, and R and C exclosures, respectively. Values are means ± 1 SE.

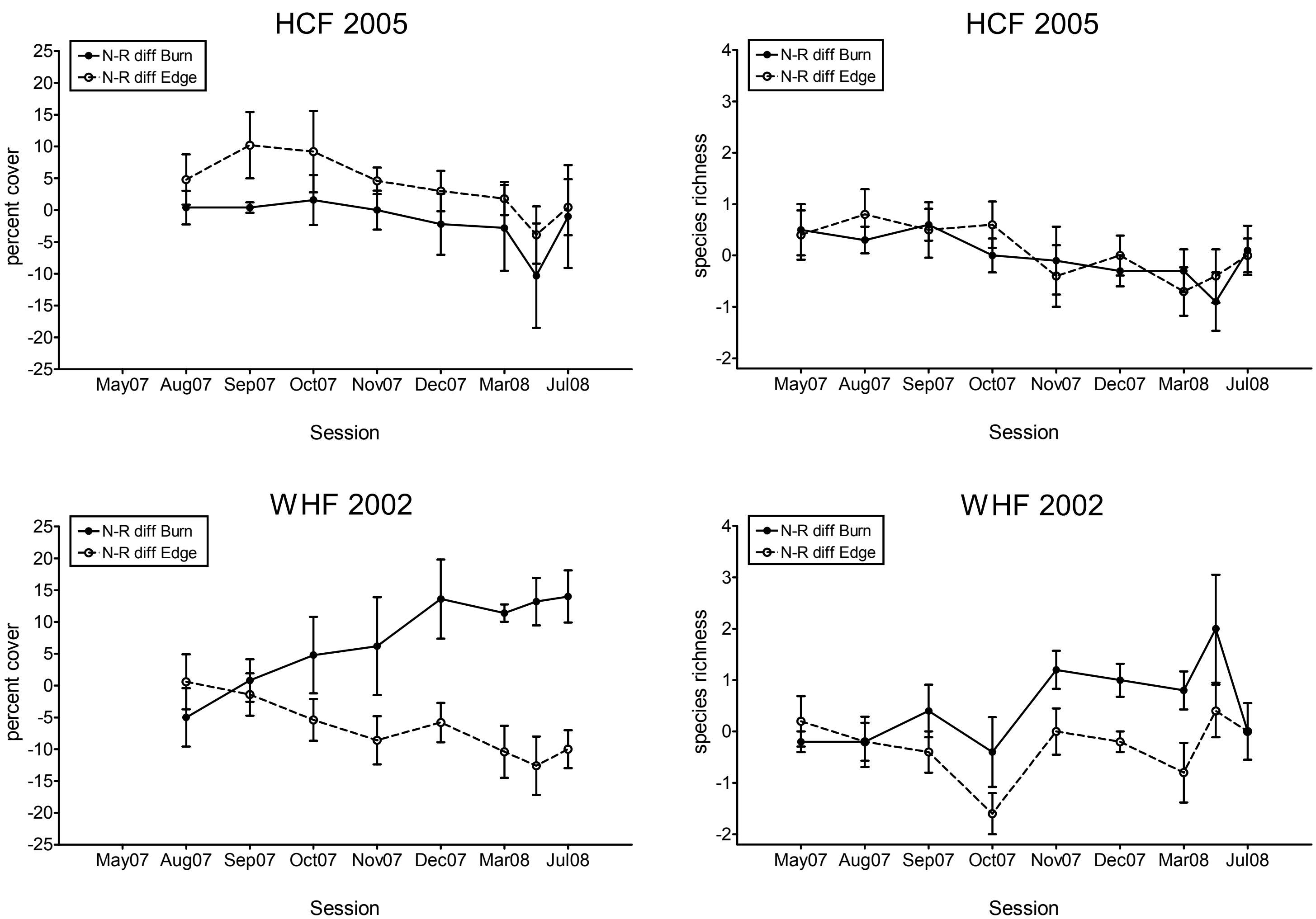


Fig. 6. The effect of small rodents on percent cover (left panels) and plant species richness (right panels) in the burn and at the burn edge in the sagebrush vegetation affected by the Hackberry Complex Fire (HCF) in 2005 and the Wildhorse Fire (WHF) 3 years earlier. The effects of rodents were calculated by subtracting values from wire cages excluding large herbivores (R) from those excluding all herbivores (N). Values are means $\pm$ 1 SE.